

## VARIABILITY IN THE PATTERN OF SEXUAL REPRODUCTION OF THE CORAL *STYLOPHORA PISTILLATA* AT EILAT, RED SEA: A LONG-TERM STUDY

B. RINKEVICH\* AND Y. LOYA

*Department of Zoology, The George S. Wise Faculty of Life Sciences, Tel Aviv University,  
Ramat Aviv 69978, Israel*

### ABSTRACT

Sexual reproduction of the Red Sea coral *Stylophora pistillata* was followed at Eilat in a long-term study (1974–1984). Field examination of over 9000 colonies through 119 months indicated that *S. pistillata* had a reproductive season of approximately 8 months (varying from 6 to 9 months). Premature planulae and eggs were aborted following winter storms, resulting in a lowering of the planular index and the number of female gonads per polyp. Histological examinations of tissue from 20 large colonies which were studied for several years, until they were found dead *in situ*, indicated that either sexuality (reproductive states) and/or fecundity could be completely altered from one reproductive season to the next: *i.e.*, hermaphroditic colonies exhibiting high fecundity in one season became male or even sterile thereafter, and vice versa. In addition, great variability in reproduction between successive years was recorded in sexuality and in the fecundity of shallow water populations. Shallow water colonies (5 m) possessed up to 5 times more female gonads per polyp and shed 5 to 20 times more planulae than deep water colonies (25 to 45 m) in which the reproductive season is 2 to 3 months shorter.

We suggest that the changes in the hermaphroditic, male, or sterile modes of reproduction in *S. pistillata* are from energy limitations and stress conditions. Since reproductive activity probably involves significant energetic expenditures, any stress or diminution in energy resources affects sexuality or fecundity. This should be considered before formulating any general hypothesis on coral reproduction.

### INTRODUCTION

Much information concerning reproductive biology of scleractinian corals has recently become available. Fadlallah (1983) reviewed past studies and provided a list of almost 90 species in which several known reproductive characteristics are presented. More recent studies (Harriott, 1983; Szmant-Froelich *et al.*, 1984; Shlesinger and Loya, 1985; Wallace, 1985; Willis *et al.*, 1985; Babcock *et al.*, 1986; Szmant, 1986) provide information on reproductive patterns of more than 100 additional species of corals.

Although this list of studied species is impressive, data on scleractinian reproduction is still scanty, especially that dealing with their reproductive ecology. These studies evaluated sizes, shapes, and numbers of gonads, and attempted to establish reproductive seasonality, lunar periodicity, mode of reproduction, planula characterizations, and behavior. However, most studies were based on observations and

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\* Present Address: Hopkins Marine Station of Stanford University, Pacific Grove, California 93950.

experiments carried out within a period of a year or less. Only a few studies dealt with longer periods ranging from two (Atoda, 1947a, b; Harriott, 1983; Jokiel, 1985; Wallace, 1985) to three years (Kojis and Quinn, 1981a; van Moorsel, 1983; Stoddard and Black, 1985). Consequently, studies on sexual reproduction often fall short in documenting many aspects of coral reproduction (Fadlallah, 1983). Detailed information on coral reproduction could clarify many aspects of their life history patterns and provide a better understanding of the coral reef as a whole.

*Stylophora pistillata* (Esper) is one of the most abundant coral species in the Gulf of Eilat, Red Sea. Some aspects of the reproduction of this species have already been studied in the field and the laboratory. Descriptions of planulae and gonads have been made (Rinkevich and Loya, 1979a). In addition, synchronization in breeding, colony size in relation to fecundity, onset of reproduction, reproduction within a single colony, and seasonality of planulation were also reported (Rinkevich and Loya, 1979b). This paper summarizes results of a ten-year study on the reproduction of *S. pistillata* which elucidate some general conclusions characterizing coral reproductive activities.

#### MATERIALS AND METHODS

Reproductive activity of *S. pistillata* was studied from March 1974 to January 1984 (most intensively from 1976 to 1980). The study area was located in front of the H. Steinitz, Marine Biological Laboratory at Eilat, Gulf of Eilat, Red Sea, and was visited regularly once a month during the ten-year study period. Large colonies (mean geometric radius,  $\bar{r} > 20$  cm) were sampled from both shallow (3–5 m) and deep water (25–60 m) populations.

Reproduction was studied by two techniques: collections of shed planulae (see below) and examinations of gonads in histological sections (Rinkevich and Loya, 1979a, b). A single branch was sampled from each colony. This branch represents the reproductive state of the entire colony (Rinkevich and Loya, 1979b). The number of female gonads was counted within serial sections for each tested polyp and quantitative data were obtained on the average number of eggs per polyp in a given specimen (6–18 polyps per sample). Male gonads were not counted because of the difficulty of following them in serial histological sections as a result of the irregular shape of a typical male gonad (Rinkevich and Loya, 1979a). Tissue samples were always taken near the bases of branches since few polyps from the tips contain genital cells (Rinkevich and Loya, 1979b; Kojis and Quinn, 1981a).

Early in the study, planulae were collected *in situ* by covering large colonies with plankton nets in the late afternoon and removing the nets at midnight (Rinkevich and Loya, 1979a). However, due to the difficulties with this technique during night diving (especially with the deep-water colonies), planulae were collected from coral branches that were brought into the laboratory. The branches were carefully removed underwater using wire cutters, and transported to the laboratory within 30 min after sampling in closed, separate plastic bags. The water in each bag was checked for the appearance of planulae. Each sample was put separately in a 5 l glass aquarium, containing filtered seawater, and left overnight. Planulae were shed during the night (Rinkevich and Loya, 1979a). Although handling stimulated planula release, it is assumed that these planulae were prepared for shedding. This assumption was supported by the finding that the released planulae were fully developed. Since conditions in all treated samples were similar, we concluded that collection procedures did not affect the results. Planulae were counted by sight and removed by pipettes. The seawater was then filtered through a plankton net (100  $\mu$ m) and all remaining planulae were

TABLE I

*Some characterizations of recorded southern storms in Eilat*

Date	No. of storms	Waves		Winds	
		Max. height (m)	Max. length (m)	General direction	Max. speed (km/h)
Feb. 1979	3	2	12	SE	nd
Apr. 1979	3	1+	nd	S	nd
Nov. 1979	1	1	6	SE	20
Dec. 1979	2	2	nd	SE	nd
Feb. 1980	2	2.5	10	SSE	35
Mar. 1980	1	nd	nd	nd	nd
Apr. 1980	1	nd	nd	nd	nd
Jan. 1981	2	1.5	20	S, SE, SW	25
Feb. 1981	3	1.2	27	SSE	18
Mar. 1981	1	0.5	nd	S, SE	nd

nd = no available data. (Personal communication, C. Porter, Israel Oceanographic and Limnological Research Ltd., Eilat).

collected and counted. Sampled branches were placed on a filter paper for 15 min to remove excess water and weighed (accuracy to the nearest 1 g). In most cases branch weights ranged between 100–200 g. Results are presented as number of released planulae per 100 g of coral skeleton, during one night.

In addition, the release of planulae from mature colonies ( $\bar{r} > 20$  cm) was checked each month *in situ* where several branches were carefully broken from many colonies. This procedure stimulated the release of planulae in colonies which were in a reproductive state. The shed planulae were easily seen and traced by sight underwater. A planular index was then formulated (see below), which took into account the relative number of planulae shed and the percentage of reproducing colonies. Since variability in the fecundity between different colonies within the population was high (Rinkevich and Loya, 1979b), up to 90 large colonies were sampled each month (in 2–3 replicates, at least 30 colonies in each) to assess the validity of the planular index. The index sign (–) was given when none of the sampled colonies released any planulae; (+–) when very few planulae were released (total number of 1–5 planulae from the 30 tested colonies in each replicate); (+) when about one third of the colonies released few planulae; (++) when up to two thirds of the colonies shed planulae (many or few; many = any small fragment broken from the colony released about two planulae); (+++) when most or all of the colonies shed planulae.

The most severe storms in the sea at Eilat are known as southern storms, which occur during the winter and spring. Some physical parameters of these storms are partly documented from February 1979 (Table I).

## RESULTS

### *Long-term study on seasonality of planulae shedding*

Planulation in *S. pistillata* was continuously studied between March 1974 to January 1984 by sampling more than 9000 colonies (Table II). The two questions investigated were whether planulation occurs in the same months from one year to the next and how the planular index in the shallow water population fluctuated during the

TABLE II

Monthly planular index in shallow water populations of *Stylophora pistillata* during 119 months of observations

Year	Planular index* in											
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1974			+++	++	++	+	-	-	-	-	-	+
1975	+	++	+++	+++	+++	++	+/-	-	-	-	+/-	+
1976	++	+++	+++	+++	+++	++	-	-	-	-	-	-
1977	-	++	+++	+++	+++	++	+	-	-	-	-	+
1978	+	++	+++	+++	++	+	+/-	-	-	-	-	-
1979	++	++	++	+++	+++	+	-	-	-	-	-	+/-
1980	+	+/-	+++	++	+++	++	+	-	-	-	-	+
1981	+	+	+++	+++	++	++	+/-	-	-	-	-	+/-
1982	++	+++	+++	+++	+++	++	-	-	-	-	-	-
1983	+	+++	+++	+++	+++	+++	+	-	-	-	-	-
1984	-											

\* (-), No planulae; (+/-), very few; (+), few; (++) intermediate; (+++), large numbers.

119 months of observations. *S. pistillata* has a long reproductive season (planulae release) lasting approximately 8 months, from December to July (Table II). However, the reproductive season ranged 6 months (in 1976) to 9 months (in 1975). In the three-month period from August to October, no planulation was ever recorded. Only once during the ten-year investigation were very few planulae observed in November (in 1975). A marked variation was noted in the December-January-February index between different years. Although these months represent the beginning of the reproductive season (Rinkevich and Loya, 1979b), this variability might also be the result of the southern storms which are most severe during the winter (Table I). This phenomenon is also demonstrated in another part of the present study: in April 1980 a southern storm interrupted our field sampling. Branch samples were collected before the storm from 10 mature colonies. Nine of them released high numbers of planulae (average of  $30 \pm 28$  planulae, per 100 g skeleton, per colony). One day after the storm samples were collected for histological study from 13 other mature colonies inhabiting the same area and depth. Only eight colonies contained low numbers of female gonads while the others were either sterile or contained only male gonads. The average number of female gonads per polyp, per colony was very low ( $0.4 \pm 0.6$ ), much lower than other April months (for more detail, see Tables VI and IV, respectively).

#### Long-term study on reproductive states

Two separate sets of experiments followed the long-term state of reproduction in shallow water populations. In the first experiment 20 large colonies ( $\bar{r} > 20$  cm) were chosen (December 1976) and sampled for histological study two to three times a year e.g., in the beginning, the peak and the end of the reproductive season over four successive reproductive periods, until the deaths of all of them were recorded (February 1980). Since synchronization in the reproduction activity exists between branches (Rinkevich and Loya, 1979b), only one branch was sampled each time from each colony. This sampling procedure did not affect survivorship or reproduction (unpub.). Colony mortality was high (Table III), although colonies were carefully chosen on the basis of their healthy state (without dead branches or tissue damage). One and



TABLE III

*Reproductive state and average number of female gonads per polyp in Stylophora pistillata colonies sampled during Dec. 1976 to Feb. 1980*

Coral no.	Average numbers of female gonads per polyp in									
	Dec. 76	Apr. 77**	Dec. 77	Apr. 78	Jun. 78	Dec. 78	Apr. 79	Dec. 79	Feb. 80	
1	-(10)	0.7 (10)*	D							
2	0.2 (10)	0.5 (10)*	D							
3	0.6 (10)	2.9 (10)*	1.2 (6)	2.6 (7)*	0.7 (6)*	-(10)	D			
4	2.4 (10)	1.4 (10)*	0.2 (6)	+(10)	D					
5	0.4 (10)	0.4 (10)*	D							
6	0.1 (10)	1.9 (10)*	+(6)	-(10)	-(10)	-(8)	D			
7	1.9 (10)	1.1 (10)*	0.5 (6)	D						
8	-(10)	D								
9	0.6 (10)	1.1 (10)*	0.7 (7)	2.2 (6)*	S					
10	-(10)	0.4 (10)*	+(6)	+(6)	-(8)	1.4 (7)	0.4 (7)	-(9)	D	
11	-(10)	D								
12	-(10)	D								
13	-(10)	2.5 (10)*	2.1 (10)	2.5 (10)*	-(6)	1.8 (6)	1.0 (8)	D		
14	-(10)	0.5 (10)*	-(5)	1.9 (11)	-(10)	-(10)	-(10)	D		
15	-(10)	1.6 (10)*	1.0 (5)	S						
16	1.1 (10)	1.3 (10)*	2.3 (10)	S						
17	-(10)	D								
18	-(10)	0.4 (10)*	D							
19	-(10)	0.9 (10)*	-(11)	3.3 (7)	S					
20	0.2 (10)	0.9 (10)*	+(7)	2.1 (8)	-(10)	1.2 (6)	D			

December and February months refer to the beginning of the reproductive season, April months to the peak of reproduction, and June to the decline phase of the reproductive season (numbers in parentheses refer to the number of polyps examined).

-, Sterile colony; +, Only male gonads present; D, The colony was found dead; \*, Planulae detected in histological sections; \*\*, Planulae were found in all plankton nets put on marked colonies; S, Destroyed by storm.

two years after the beginning of the study, 60% and 30%, respectively, of the colonies were alive. Only one colony of the 20 samples (5%) remained alive after 3 years (Table III). A decrease in fecundity was repeatedly observed several months prior to the natural death of many of the colonies. In four out of the six dead colonies following a period of high fecundity (colonies 9, 15, 16, 19; Table III), the death was attributed to southern storms. None of the dead colonies during the first 4 months of the study (colonies 8, 11, 12, 17; Table III) contained any genital cells when first sampled.

The results (Table III) also indicate variability in sexuality (reproductive states: male, hermaphrodite, or sterile modes of reproduction) and fecundity of a specific colony in different years. Hermaphroditic colonies which exhibit high fecundity in one reproductive season may differ in the following reproductive season in which they become sterile (colonies 6, 14; Table III), or male (colonies 4, 10; Table III) and vice versa. The changes in colony reproductive patterns are further demonstrated in colonies sampled in three to four consecutive December months (colonies 3, 6, 10, 13, 14, 20; Table III). Sexuality or fecundity of five out of these six colonies were altered in each December month.

In the second set of experiments (Table IV), 155 large shallow water colonies were sampled over 10 successive sampling periods at the beginning and during the peak of 5 reproductive seasons (April 1976–April 1980). Changes among the different seasons

TABLE IV

*Stylophora pistillata: reproductive states of shallow water populations*

Date	No. of colonies	Colony reproductive state (%)			Average female gonads (polyp <sup>-1</sup> colony <sup>-1</sup> )
		Hermaphrodites	Males only	Sterile	
Apr. 76	17	94	6	—	1.5 ± 0.9
Dec. 76	20	45	—	55	0.4 ± 0.7
Apr. 77	16	100	—	—	1.2 ± 0.8
Dec. 77	12	67	25	8	0.7 ± 0.8
Apr. 78	9	67	22	11	1.6 ± 1.3
Jun. 78	16	31	—	69	0.2 ± 0.4
Dec. 78	14	50	—	50	0.5 ± 0.6
Mar. 79	26	88	—	12	1.5 ± 1.1
Dec. 79	12	50	25	25	0.5 ± 0.7
Apr. 80	13	62	—	38	0.4 ± 0.6

either in sexuality or fecundity were observed. For example, each one of the 4 different December months (years 1976, 1977, 1978, 1979) represented different patterns of reproductive states: 8–56% of the colonies were sterile, 0–25% males and 45–67% were hermaphrodites among the different December months. The same pattern was recorded for sexuality of March to April months: 0–38%, 0–22% and 62–100%, respectively (Table IV). It is concluded that “one year of sampling” is not enough for the characterization of reproductive states in this species.

#### *Reproduction in shallow versus deep water populations*

Possible differences in reproduction between shallow and deep water populations were tested in two sets of experiments. In the first, we analyzed serial histological sections of 90 shallow water colonies (from Table IV). The results were compared to those of 77 deep water colonies (25–45 m, Table V) sampled on the same days during three successive reproductive seasons (April 1978–April 1980). Shallow water colonies possessed up to 5 times more female gonads per polyp per colony than deep water colonies ( $P < 0.01$ , Wilcoxon's signed rank test; Sokal and Rohlf, 1981). This phenomenon was most clear during the peak of the reproductive season, March to

TABLE V

*Stylophora pistillata: reproductive states of deep water colonies*

Date	Depth (m)	No. of colonies	Colony reproductive state (%)			Average female gonads (polyp <sup>-1</sup> colony <sup>-1</sup> )
			Hermaphrodites	Males only	Sterile	
Mar. 78	60	1	100	—	—	0.7
Apr. 78	25–30	15	40	40	20	0.3 ± 0.4
Jun. 78	25	15	7	—	93	0.0 ± 0
Dec. 78	27–30	15	86	7	7	0.7 ± 0.6
Mar. 79	40–45	11	36	36	28	0.4 ± 0.8
Dec. 79	27–30	9	—	—	100	0
Apr. 80	25–30	12	8	50	42	0.0 ± 0.1

TABLE VI

*Shed planulae in sample branches of shallow and deep water Stylophora pistillata colonies*

Date	Shallow				Deep			
	Depth (m)	No. of colonies	Colonies which shed planulae (%)	Average no. of planulae (per 100 g skeleton)	Depth (m)	No. of colonies	Colonies which shed planulae (%)	Average no. of planulae (per 100 g skeleton)
Jan. 79	3-6	5	80	32 ± 49	27	6	0	0
Feb. 79	3-6	6	100	85 ± 95	27-30	4	25	1 ± 1
Mar. 79	5	6	100	22 ± 20	40-42	5	20	0.4 ± 1
Jun. 79	5	4	100	31 ± 22	34	5	20	2 ± 5
Dec. 79	5	4	0	0	30	3	0	0
Jan. 80	3-5	9	89	14 ± 31	39-42	9	33	4 ± 10
Feb. 80	5	6	83	4 ± 2	30	6	0	0
Apr. 80	3-6	10	90	30 ± 28	25-27	9	44	3 ± 6
May 80	3-8	10	90	44 ± 47	27	10	70	4 ± 7
Jun. 80	6-9	10	100	14 ± 10	27-30	10	30	3 ± 7
Jul. 80	4-6	10	70	3 ± 6	30	10	20	0.2 ± 0.4
Jan. 81	3-5	5	60	4 ± 8	30-35	5	0	0
Feb. 81	3-5	6	67	5 ± 3	27-30	6	33	1 ± 1

April (the average female gonad per polyp in April 1980 is lower than other April months because samples were taken immediately after a storm).

In the second set of experiments, planulae were collected in the laboratory from branch samples of 91 shallow water and 88 deep water colonies, on 13 collecting dates (Table VI). Significantly more planulae were shed by shallow water colonies than by deep water colonies ( $P < 0.01$ ; Wilcoxon's signed rank test; Sokal and Rohlf, 1981). At the peak of the reproductive season about 20-80 planulae on average were shed per 100 g skeleton from shallow water colonies during one night. In deep water colonies the number did not exceed four planulae. An additional 55 deep water colonies were sampled during summer and fall (July-November) to examine whether the reproductive season there differs from that of shallow water populations. All histological sections were free of eggs. Moreover, no planulae were shed during a parallel study where branches were carefully broken *in situ* from an additional 80 colonies. These results indicate that the reproductive season of deep water colonies is probably two to three months shorter than that of shallow water populations.

## DISCUSSION

The study of coral reproductive biology may be engaged with ambiguous definitions which could lead to wrong interpretations. For example, Fadlallah (1983) indicated that confusion arises from the applications of the term hermaphroditism, which describe two different life history processes: (1) development of monoecy over the lifetime of a specimen and, (2) sequential maturation of female and male products within one breeding period. Thus, it was accepted that *S. pistillata* (Rinkevich and Loya, 1979a, b) and *Goniastrea australensis* (Kojis and Quinn, 1981a, b) were protandrous hermaphrodites over their lifetime, but protogynous hermaphrodites in each single reproductive season. The present study indicates that either sexuality and/or fecundity may be completely altered from one reproductive season to the next. Her-

hermaphroditic colonies which exhibited high fecundity in one season became male or even sterile thereafter, and vice versa. Small colonies (geometric mean radius  $\bar{r} < 2$  cm) which invest much energy in rapid growth (Loya, 1985), possess only male gonads in their first year of reproduction. An increase in colony size correlated with an increase in percentage of hermaphroditic colonies within the population (Rinkevich and Loya, 1979b). Reproduction of injured colonies of *S. pistillata* which invested energy in growth and regeneration was significantly reduced for at least two successive reproductive seasons after the fracturing event (Rinkevich, 1982). In addition, the fecundity of dying colonies was reduced several months before their death (Table III and Rinkevich and Loya, 1986), and dying colonies often changed their sexuality before their mortality and became male. Field experiments also demonstrated that the number of female gonads per polyp in *S. pistillata* was significantly reduced in colonies competing intraspecifically and the typical synchrony in reproduction among different branches of a given colony was changed and desynchronized (Rinkevich and Loya, 1985).

From the above results, we suggest that sexuality and fecundity in *S. pistillata* are responsive to the general state of health of the colony and its energetic limitations.

Studies also addressed reproduction/energy allocation questions in other coral reef species. Kojis and Quinn (1985) found lower fecundity in damaged *Goniastrea favulus* colonies compared to unharmed controls and suggested that this resulted from reallocation of resources to growth activities that would repair damaged tissue and cover the broken skeletons. Richmond (1984) indicated that reef corals may allocate energy into new tissue via budding for colony growth, or via planulation for production of new colonies. He found that colonies of *Pocillopora damicornis* at Enewetak atoll, Marshall Islands, allocated the majority of their reproductive energy into larva production while in the eastern Pacific the same species channels energy into colony growth. Thus, internal and/or external (see below) determinants may play a significant role in the expression of sexuality or fecundity in hermatypic corals, although the mechanisms are not yet understood.

Stimson (1978) proposed that coral species which release planulae are characteristic of shallow water environments such as reef flats, and hypothesized that shallow water species should planulate to facilitate early settlement in the parental habitat. Conversely, deep water corals should release eggs and sperm into the water to facilitate dispersal. More recent studies, however, suggest that the mode of reproduction is related to more complex factors than habitat alone (Harriott, 1983; Szmant, 1986). Thus it is of interest to study the mode of reproduction of the same species in two different depths. Karlson (1981) found a reduction in reproductive activity with increasing depth in two Jamaican species of *Zoanthus*. Kojis and Quinn (1983) further indicate that fecundity of *Acropora palifera* decreased with depth. Colonies at depths greater than 12 m had approximately half the fecundity of surface colonies. These studies support the results of the present study (Tables IV, V, VI) which indicate high differences in fecundity between shallow and deep water *S. pistillata* colonies.

The importance of available energy for reproduction is apparent from the decrease of fecundity in deep water populations. *S. pistillata* invests photosynthetically derived energy in reproduction (Rinkevich, 1982; Rinkevich and Loya, 1983). McCloskey and Muscatine (1984) found that the daily CZAR (the percentage contribution of zooxanthellae-translocated carbon to animal maintenance respiration) in *S. pistillata* in deep water was less than half of that in shallow water. Mean CZAR at 35 m was 78%, compared to 157% at 3 m. They also found that the decreased carbon availability to the host animal at 35 m was the consequence of both decreased net carbon fixation and decreased percentage of net fixed carbon translocated to the host.



Therefore, we suggest, that the generous daily carbon supply in shallow water colonies enables them to channel significantly more energy to reproduction than deep water colonies.

It is hard to separate the two explanations for the differences in reproductive activity between shallow and deep water colonies *e.g.*, energy limitations *versus* selective pressures. The present results point to energy limitation in deep water colonies rather than to the suggestion of selection pressures which favor high fecundity of shallow water colonies (Stimson, 1978).

This study provides for the first time results of long-term (1974–1984) experiments and observations on reproductive activities in a hermatypic coral. These and earlier (Rinkevich, 1982; Rinkevich and Loya, 1985; 1986) results indicate that sexuality as well as fecundity are determined and regulated by a variety of internal processes (such as the state of health of the colony, regeneration of broken branches, energy limitation, senescence, and death) and external, physical parameters (such as storm activities). The only other relevant papers on external parameters are the recent works of Jokiel (1985) and Jokiel *et al.* (1985) who suggested that environmental factors including temperature, salinity, tidal cycle, visible, and ultraviolet radiation influence the number of planulae released by *Pocillopora damicornis* per spawning cycle, as well as the synchronization of lunar release of planula larvae. Therefore it is concluded that reproductive activity in *S. pistillata* involves significant energetic expenditures that otherwise would be allocated into other physiological pathways such as growth and maintenance. As a result, any significant stress or diminution in energy resources affects at least one of the reproductive characteristics of this species. Physical and biological parameters have often been directly related to the distribution of a given species. However, the present study indicates that even reproduction can be directly altered as a result of the influence of these parameters. The changes in the reproductive activity of *S. pistillata* colonies in the field may not be a function of a single parameter. The combined effect of several external and internal factors on gravid colonies should be examined experimentally before and during the reproductive season. These should be considered before formulating any general hypothesis on coral reproduction.

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#### LITERATURE CITED

- ATODA, K. 1947a. The larva and postlarval development of some reef building corals. I. *Pocillopora damicornis cespitosa* (Dana). *Sci. Rep. Tohoku Univ. (4th ser.)* **18**: 24–47.
- ATODA, K. 1947b. The larva and post larval development of some reef building corals. II. *Stylophora pistillata* (Esper). *Sci. Rep. Tohoku Univ. (4th ser.)* **18**: 48–64.
- BABCOCK, R. C., G. D. BULL, P. L. HARRISON, A. J. HEYWARD, J. K. OLIVER, C. C. WALLACE, AND B. L. WILLIS. 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Mar. Biol.* **90**: 379–394.

- FADLALLAH, Y. H. 1983. Sexual reproduction, development and larval biology in scleractinian corals. A review. *Coral Reefs* 2: 129-150.
- HARRIOTT, V. J. 1983. Reproductive ecology of four scleractinian species at Lizard Island, Great Barrier Reef. *Coral Reefs* 2: 9-18.
- HARRISON, P. L., R. C. BABCOCK, G. D. BULL, J. K. OLIVER, C. C. WALLACE, AND B. L. WILLIS. 1984. Mass spawning in tropical reef corals. *Science* 223: 1186-1189.
- JOKIEL, P. L. 1985. Lunar periodicity of planula release in the reef coral *Pocillopora damicornis* in relation to various environmental factors. Pp. 307-312 in *Proc. 5th Int. Coral Reef Congr.* Vol. 4, C. Cabrie and B. Salvat, eds. Tahiti.
- JOKIEL, P. L., R. Y. ITO, AND P. M. LIU. 1985. Night irradiance and synchronization of lunar release of planula larvae in the reef coral *Pocillopora damicornis*. *Mar. Biol.* 88: 167-174.
- KARLSON, R. H. 1981. Reproductive patterns in *Zoanthus* spp. from Discovery Bay, Jamaica. Pp. 699-704 in *Proc. 4th Int. Coral Reef Symp.*, Vol. 2, E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh, Jr., and R. T. Tsuda, eds. Manilla.
- KOJIS, B. L., AND N. J. QUINN. 1981a. Aspects of sexual reproduction and larval development in the shallow water hermatypic coral, *Goniastrea australensis* (Edwards and Haime, 1857). *Bull. Mar. Sci.* 31: 558-573.
- KOJIS, B. L., AND N. J. QUINN. 1981b. Reproductive strategies in four species of *Porites* (Scleractinia). Pp. 145-151 in *Proc. 4th Int. Coral Reef Symp.*, Vol. 2, E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh, Jr., and R. T. Tsuda, eds. Manilla.
- KOJIS, B. L., AND N. J. QUINN. 1983. Coral fecundity as a biological indicator of reef stress. *Am. Zool.* 23: 961.
- KOJIS, B. L., AND N. J. QUINN. 1985. Puberty in *Goniastrea favulus*. Age or size limited? Pp. 289-293 in *Proc. 5th Int. Coral Reef Congr.* Vol. 4, C. Cabrie and B. Salvat, eds. Tahiti.
- LOYA, Y. 1985. Seasonal changes in growth rate of a Red Sea coral population. Pp. 187-191 in *Proc. 5th Int. Coral Reef Congr.* vol. 6, C. Cabrie and M. Harmelin-Vivien, eds. Tahiti.
- MCCLOSKEY, L. R., AND L. MUSCATINE. 1984. Production and respiration in the Red Sea coral *Stylophora pistillata* as a function of depth. *Proc. R. Soc. Lond. B* 222: 215-230.
- VAN MOORSEL, G. W. N. M. 1983. Reproductive strategies in two closely related stony corals (*Agaricia*, Scleractinia). *Mar. Ecol. Prog. Ser.* 13: 273-283.
- RICHMOND, R. H. 1984. An energetic approach relating fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. *Am. Zool.* 24: 27A.
- RINKEVICH, B. 1982. *Stylophora pistillata*. Ecophysiological aspects in the biology of a hermatypic coral. Ph.D. thesis, Tel Aviv University, Israel. 300 pp. (in Hebrew with English summary).
- RINKEVICH, B., AND Y. LOYA. 1979a. The reproduction of the Red Sea coral *Stylophora pistillata*. I. Gonads and planulae. *Mar. Ecol. Prog. Ser.* 1: 133-144.
- RINKEVICH, B., AND Y. LOYA. 1979b. The reproduction of the Red Sea coral *Stylophora pistillata*. II. Synchronization in breeding and seasonality of planulae shedding. *Mar. Ecol. Prog. Ser.* 1: 145-152.
- RINKEVICH, B., AND Y. LOYA. 1983. Short term fate of photosynthetic products in a hermatypic coral. *J. Exp. Mar. Biol. Ecol.* 73: 175-184.
- RINKEVICH, B., AND Y. LOYA. 1985. Intraspecific competition in a reef coral: effects on growth and reproduction. *Oecologia* 66: 100-105.
- RINKEVICH, B., AND Y. LOYA. 1986. Senescence and dying signals in a reef building coral. *Experientia* 40: 320-322.
- SHLESINGER, Y., AND Y. LOYA. 1985. Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. *Science* 228: 1333-1335.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman, NY. 859 pp.
- STIMSON, J. S. 1978. Mode and timing of reproduction in some common hermatypic corals from Hawaii and Enewetak. *Mar. Biol.* 48: 173-184.
- STODDARD, J. A., AND R. BLACK. 1985. Cycle of gametogenesis and planulation in the coral *Pocillopora damicornis*. *Mar. Ecol. Prog. Ser.* 23: 153-164.
- SZMANT, A. M. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5: 43-53.
- SZMANT-FROELICH, A., L. RIGGS, AND M. REEUTTER. 1983. Sexual reproduction in Caribbean reef corals. *Am. Zool.* 23: 961.
- WALLACE, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Mar. Biol.* 88: 217-233.
- WILLIS, B. L., R. C. BABCOCK, P. L. HARRISON, J. K. OLIVER, AND C. C. WALLACE. 1985. Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. Pp. 343-348 in *Proc. 5th Int. Coral Reef Congr.* Vol. 4, C. Cabrie and B. Salvat, eds. Tahiti.